

Application of marine reserves to reef fisheries management

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Abstract Establishing permanent 'no-take' marine reserves, areas where fishing and all other extractive activities are prohibited, is an attractive but under-utilized tool for fisheries management. Marine reserves could potentially deal with many fishery problems that are not effectively addressed by other traditional management measures; they also offer numerous social, economic, and scientific benefits not directly related to fisheries. Limited but growing research has shown beneficial biological and economic effects of marine reserves on fisheries. More research is needed, especially at larger scales, to determine the ideal marine reserve size, number and location necessary to optimize fisheries productivity and resource conservation. Sufficient evidence is available to justify the expanded use of marine reserves in an adaptive approach to fisheries management.

Key words: biodiversity, conservation, coral reefs, ecosystem, no-take, refuge.

INTRODUCTION

For Reefish '95, I was requested to provide a critical analysis of what marine reserves can and cannot do, and what we know and need to know to use them effectively. Marine reserves protect resources in specific areas by prohibiting all fishing, harvesting and other extractive activities, such as mining and petroleum removal. Formal use of marine reserves has grown rapidly since the first ones were established in New Zealand and Australia in the 1970s (Ballantine 1991; Bohnsack 1996). Most existing reserves are small (less than a few km²) and are used primarily for conservation and tourism. They occur in both small and large countries where levels of compliance and enforcement vary greatly (Alder 1996). Most reserves occur in tropical and subtropical regions, although interest in their use in temperate regions is growing (Shackell & Willison 1995).

Serious consideration of marine reserves as a fisheries management tool has developed only recently (Plan Development Team (PDT) 1990; Roberts & Polunin 1991; Dugan & Davis 1993; Rowley 1994), mostly as the result of (i) international legal changes allowing coastal countries greater control over their marine resources (Bohnsack 1996); (ii) increased research showing beneficial effects of marine reserves (Cole *et al.* 1990; Dugan & Davis 1993; Roberts & Polunin 1993; Holland & Brazee 1996); and (iii) frequent failures of fisheries managed by other manage-

ment methods (Dayton *et al.* 1995; Roberts *et al.* 1995; Savina 1995; Appeldoorn 1996; Bohnsack 1996; Holland & Brazee 1996; Roberts 1997).

Fisheries have collapsed in countries independent of resource wealth, education level, and quantity and quality of fisheries data (FAO 1994). The reasons for fishery failures are numerous. In many cases, greed, ignorance and stupidity overwhelmed scientific advice and common sense (Kunzig 1995), while in others, inadequacy of scientific models, environmental variability, ignorance about natural systems, poor data, inadequate compliance with fishery regulations and short-term economic considerations led to fishery collapses (Ludwig *et al.* 1993; Bohnsack & Ault 1996). A common problem is that most fisheries models have been developed for single species stocks in temperate environments and are not suitable for complex multispecies and multigear, tropical fisheries. Simple mathematical models may not adequately describe or predict complex natural interactions between species, the environment and human behaviour (Roberts 1997). Also, the hope of being able to understand and manipulate systems, at will, is probably the height of human arrogance and folly (Holling & Meffe 1996).

MARINE RESERVES

Conceptually, marine reserves provide populations a spatial refuge from harvest while more traditional fishery management methods attempt to provide a numerical refuge by allowing a sufficient portion of the

population to escape harvest in order to reproduce. This escape is accomplished by either dictating size limits or reducing fishing mortality through control of fishing effort. Typical measures include minimum size limits, quotas, bag limits, fishing gear restrictions, trip limits, seasonal closures and limited entry to the fishery (Munro & Williams 1985). Unfortunately, size limits and effort controls are frequently circumvented and ineffective (Waters 1991).

The creation of marine reserves in representative and critical habitats can provide formal spatial protection for fishery stocks. Historically, many fisheries have probably benefited from natural spatial refuges: areas too deep, too remote, too hard to locate or otherwise inaccessible to fishing (Dugan & Davis 1993; Lozano-Alvarez *et al.* 1993). With advancements in fishing technology, these natural refuges have disappeared or become ineffective over time.

Marine reserves also provide many non-fishery benefits while allowing fisheries to operate in surrounding areas (Bohnsack 1993). These benefits include: improving conservation through the protection of biodiversity and ecosystem structure, function and integrity; increasing the knowledge, understanding and appreciation of marine ecosystems; and creating opportunities for non-consumptive human activities (Table 1). Many of these benefits, such as protecting marine biodiversity, are incompatible with full exploitation or are not addressed by traditional fisheries management measures.

Marine reserves have many potential fishery benefits (Table 2). The most important direct benefits include: exporting eggs and larvae to surrounding fishing grounds; exporting biomass by migration of juveniles and adults; protecting population genetics from selective fishing; protecting against stock collapse from fishing; and assuring a more rapid recovery if stocks collapse outside reserves. Fisheries can indirectly benefit from: improved fishery models using fishery-independent data from undisturbed areas; an increased understanding of marine ecosystems; and a more holistic, ecosystem-based approach to fishery management. While some fishery benefits have been empirically demonstrated, many have been deduced based on reasonable assumptions or speculations that require further evaluation (see reviews by Roberts & Polunin 1991, 1993; Carr & Reed 1993; Dugan & Davis 1993; Towns & Ballantine 1993; Rowley 1994; Bohnsack 1996; Table 2).

Because of limitations, marine reserves are not a panacea for all fishery problems (PDT 1990). Species that are highly migratory or that have large home ranges are unlikely to receive much protection from small reserves (Roberts 1997). In most regions, sufficient scientific information is not available to optimally design marine reserves. Closing areas to fishing can cause short-term and long-term cultural, social and economic disruption, particularly in heavily exploited areas.

Table 1. Non-fishing benefits of marine reserves

Protect ecosystem structure, function, and integrity

Protect physical habitat structure from fishing gear and other anthropogenic impacts
 Protect biodiversity at all levels:
 Restore population size and age structure
 Restore community composition (species presence and abundance)
 Protect genetic structure of populations from direct and indirect fisheries selection
 Protect ecological processes from effects of exploitation:
 Maintain abundance of keystone species
 Prevent cascading ecosystem effects
 Prevent threshold effects
 Prevent second-order effects
 Maintain food web and trophic structure
 Ensure system resilience to stress
 Maintain high quality feeding areas for fish and wildlife
 Leaves less room for irresponsible development
 Permits distinguishing natural from anthropogenic changes
 Promotes ecosystem management
 Encourages holistic approach to management

Increased knowledge and understanding of marine systems

Provides long-term undisturbed monitoring sites
 Provides focus for study
 Provides continuity of knowledge in undisturbed sites
 Provides opportunity to restore or maintain natural behaviours
 Reduces risks to long-term experiments
 Provides experimental sites needing natural areas
 Provides cumulative understanding from multiple studies at one site over time
 Provides synergism of knowledge by relating studies in different disciplines at one site over time
 Provides natural reference areas for assessing anthropogenic impacts (including fisheries)
 Provides undisturbed natural sites for certain experiments
 Provides sites for enhanced primary and adult education
 Provides sites for high-level graduate education

Improves non-consumptive opportunities

Enhances and diversifies economic opportunities
 Enhances and diversifies social activities
 Enhances personal satisfaction by:
 Improving peace-of-mind for naturalists, conservationists, and other passive users;
 Enhancing aesthetic experiences
 Enhancing spiritual connection to natural resources
 Enhances non-consumptive recreational opportunities
 Creates opportunities for wilderness experiences
 Enhances educational opportunities
 Promotes ecotourism
 Improves appreciation of conservation
 Increases sustainable employment opportunities
 Creates public awareness about environment
 Stabilizes the economy

Adapted from PDT (1990) and unpublished proceedings of a 1995 meeting by the Center for Marine Conservation (J. Sobel pers. comm. 1995).

Table 2. Levels of scientific support for potential fishery benefits**Well supported**

Increase abundance of overfished stocks (inside reserves)
 Reduce overfishing of vulnerable species
 Reduce bycatch mortality (inside reserves)
 Reduce incidental fishing mortality
 Simplifies enforcement and compliance
 Reduce conflicts between users
 Provide some resource protection without data or other information
 Reproduction
 Increases spawning stock biomass
 Increases density of spawning individuals in reserves
 Provides undisturbed spawning conditions, habitats etc.
 Increases spawning potential and stock fecundity

Partially supported or based on established principles

Provide spillover of juveniles and adults
 Reduce chance of recruitment overfishing
 Accelerate stock recovery after collapses
 Facilitate stakeholder involvement in fisheries management
 Provide data for improved fisheries management
 Increases public understanding and acceptance of fishery management
 Reproduction
 Increases egg and larval production

Unproven, untested or inadequately tested

Increase abundance of overfished stocks (outside reserves)
 Maintain diversity of fishing opportunities
 Protect intraspecific genetics from fishery selection
 Maintain sport trophy fisheries
 Reduce variance in yield
 Allows increased fishing mortality outside of reserves
 Reduce impacts of environmental variability on fisheries
 Reproduction
 Enhances recruitment

Adapted from PDT (1990) and unpublished proceedings of a 1995 meeting by the Center for Marine Conservation (J. Sobel pers. comm. 1995).

Once established, compliance and enforcement must be adequate for benefits to accrue (Jennings *et al.* 1996). In some cases, closures may primarily benefit fisheries in other countries because of dispersal patterns and oceanographic conditions. Recent experience shows that establishing reserves sufficiently large to demonstrate fishery benefits is difficult because of resistance to using new fishery management approaches and intense political opposition from local special interests (Roberts *et al.* 1995; Bohnsack & Ault 1996; Bohnsack 1997).

RESEARCH NEEDS

More research is needed on the design, costs and benefits of marine reserves. Although some proposed

benefits have been demonstrated, others require verification or further testing (Table 2). Further research is needed to identify what species can benefit from marine reserves and how reserves can be used in multispecies fisheries. While there is good evidence that reserves can benefit sedentary species, little attention has been given to pelagic or migratory species. Some studies have suggested that benefits may accrue to species once considered too mobile to benefit from marine reserves, such as spiny lobster *Panulirus argus* (Davis & Dodrill 1980) and *Jasus edwardsii* (MacDiarmid & Breen 1992), and the carangid (*Caranx melampygus*; Holland & Brazee 1996). Most studies of marine reserves have examined effects on tropical coral reefs. Their potential fisheries role in more temperate environments deserves greater attention. Some of the most important research topics are discussed below.

Size and total area

The effectiveness of marine reserves will depend on species and the size, total number, total area and reserve location. Despite the growing number of reserves around the world, few were established primarily for fisheries purposes and few have been adequately monitored to evaluate their effectiveness for fisheries use (Jennings *et al.* 1996; Russ & Alcala 1996b). Studies of larger reserves are especially needed because most existing reserves are probably too small to have demonstrable regional fishery benefits (e.g. Ramos-Espla & McNeill 1994).

Some scientific agreement exists that reserves should include representative areas of all habitats. A major fisheries concern is that reserves could be too small, too few, cover too little total area or be located in the wrong areas to be effective. Research on the conservation tradeoffs between using a single large or several small reserves (known as the SLOSS problem) is generally lacking in marine systems although it has been a focal point in terrestrial conservation (Simberloff & Abele 1976; Shafer 1990). Because most marine organisms have high fecundity and dispersal capabilities, a network of multiple small reserves may be preferable to a few large reserves, as long as they are sufficiently large to retain reproductive populations (Townes & Ballantine 1993; McClanahan 1994).

The total area to be included in marine reserves is an important problem. Protecting a minimum of 10–20% of the total area of all representative habitats has been recommended based on cultural traditions, social acceptability, and the precautionary (conservation) principle (Ballantine 1991; Dayton *et al.* 1995). Larger targets of 20–30% of total area have been recommended based on goals of maintaining stock spawning potential ratios (SPR; the ratio of egg output under fished conditions to that of an unexploited stock) at levels necessary to prevent overfishing (PDT 1990;

Roberts *et al.* 1995). These figures could be adjusted depending on the measured success of other fishery management measures for protecting SPR and the amount of migration out of reserves. Some preliminary research has suggested that protecting a large total area (~50%) may be possible, with little impact on total yield, if fishing effort is increased outside reserves (Nowlis 1995).

Location and dispersal

Demonstrating that marine reserves can prevent or reduce the chances of fishery collapse is especially important. Although marine reserves can protect resources inside their boundaries, their contribution to surrounding areas is less clear (Russ & Alcala 1994). Benefits from adults and juveniles migrating out of reserves are likely to have local effects on fisheries (Attwood & Bennet 1994; Russ & Alcala 1996a), while export and dispersal of eggs and larvae outside reserves are more likely to have regional effects (Stoner & Ray 1996). Specific research on the many spatial reserves established to protect single species or to eliminate specific fishing gears has been mostly overlooked in terms of its general application to marine reserves (Bohnsack 1996).

One of the most important applied fishery research questions is to identify the contribution of reserves to larval dispersal and recruitment (Carr & Reed 1993). In particular, identifying larval source and sink areas would greatly facilitate designing and locating reserves (Pulliam 1988; Dayton *et al.* 1995). Source areas are net exporters of individuals, while sink areas are net recipient areas in which within-habitat reproduction is insufficient to balance local mortality. In theory, fewer or smaller reserves would be required if they included larval source areas. Developing predictive models will be challenging because of the need to couple biotic and abiotic factors and the need to adequately consider environmental and biological variability.

Genetic biodiversity

The potential adverse impacts of selective fishing on the genetic biodiversity of exploited populations are a growing management concern but difficult to examine (Thorpe *et al.* 1981; Nelson & Soule 1987; Bergh & Getz 1989; Parma & Deriso 1990; Buxton 1993; Miller & Kapuscinski 1994; Sheridan 1995). Only recently have tools been developed to evaluate genetic changes (Shulman & Bermingham 1995) and, because most fisheries have been exploited for decades to centuries, past genetic changes may be obscured (Halas & Reitz 1992). Conducting controlled experiments is difficult (McAllister & Peterman 1992). Despite these problems, growing evidence shows adverse genetic changes

in some fish populations due to human activities (Montgomery 1983; Sheridan 1995).

Fishing can reduce genetic heterozygosity (Bergh & Getz 1989) and lead to potentially adverse genetic selection on average size, growth rates, maturity (Ricker 1981) and behaviour (Wilson & Clarke 1996). Loss of genetic diversity has been shown in orange roughy, *Hoplostethus atlanticus*, off New Zealand after only 6 years of exploitation in which approximately 70% of the biomass had been removed (Smith *et al.* 1991). Reef fishes could be particularly vulnerable to selective fishing where fishing mortality rates are high because of their life-history characteristics, which include long lives, delayed reproduction, slow growth and aggressive behaviour (Travis 1989; PDT 1990).

By protecting population segments of sedentary species from fishery selection, marine reserves could help maintain the genetic biodiversity of wild populations (PDT 1990). Characters vulnerable to selection can maintain their natural advantages inside reserves and would continue to be dispersed to surrounding fished populations. This potential reserve benefit remains mostly speculative and needs to be demonstrated. It will be especially important to assess and model species with different life-history traits and different vulnerabilities to fishing. Over time, genetic characters inside and outside of reserves could diverge.

Ecosystem management

Frequent fishery failures have led to widespread calls for moving from single-species to ecosystem management (Murawski 1991; Apollonio 1994; National Research Council 1994; Angermeier & Schlosser 1995; Christensen *et al.* 1996). To make this transition, permanent 'no-take' marine ecological reserves will be necessary to provide essential reference areas to evaluate impacts of fishing and other extractive human activities on the ecosystem and to allow a better understanding of ecosystem structure, function and performance (McClanahan & Mutiga 1988). In reserves, natural variability, trophic interactions, behaviour, natural mortality and other essential ecological factors can be examined with minimum human disturbance. Presently, conducting basic research is difficult or impossible for many exploited species because of interference from fishing. Reserves provide monitoring sites so that natural long-term changes can be distinguished from anthropogenic changes (Davis 1989). Marine reserves also may be the only practical way to allow ecosystems to exhibit the full range of natural variability essential for their persistence (Duran & Castilla 1989; Holling & Meffe 1996). More research is needed to develop practical ecosystem-fishery models (McClanahan 1995).

The human dimension

Social and economic considerations are important for successful establishment and acceptance of marine reserves (Tisdell & Broadus 1989; Alder *et al.* 1994; Cole-King 1995; Gubbay 1995). Further research is needed on fishery costs and benefits. One of the top concerns is the removal of areas from fishing access which results in the 'not in my backyard' (NIMBY) problem. Fortunately, political processes are reasonably good at solving this type of problem, which is why facilities exist that are important but which nobody wants nearby, such as power plants, airports, prisons and industrial parks. Establishing marine reserves may be simpler because private property usually does not have to be purchased. Research is still needed on ways to reduce detrimental short-term impacts until long-term benefits can accrue, especially in fully exploited or overfished fisheries (Bohnsack 1994). If large reserves are needed, perhaps phasing in small areas over time could mitigate detrimental impacts. A modelling approach may be appropriate for this problem. In many cases, acceptance of marine reserves may be facilitated with education and direct local experience (Russ & Alcala 1994; Wolfenden *et al.* 1994).

Because marine reserves offer a holistic approach to a variety of problems, appropriate technical models have not been developed for their use. This shortage hinders the application of marine reserves. In some cases, managers appear to demand higher standards of supporting evidence for using marine reserves compared to more traditional management measures. Most fishery management is done in an adaptive management sense of trial and error, and rarely are measures 'proven' to be effective before being applied. Demands of 'proof' that marine reserves will be effective before using them creates a paradox, in that to demonstrate effectiveness some marine reserves must be established. Some empirical research is necessary because of the expected influence of local conditions. This paradox has impeded greatly the scientific advancement and the application of marine reserves. Apparently, the hope is that someone else will take the risks and do the necessary research first. Unfortunately, many countries do not have necessary economic and human resources to do the necessary research.

In some cases resistance to using marine reserves occurs simply because traditionally they have not been used in fisheries (PDT 1990). This bias is often reflected in policies that resist the use of marine reserves until all other options have been shown to fail. This approach greatly increases the risk of fishery collapse and significantly extends the recovery time necessary to restore depleted areas (Russ & Alcala 1996b). Experimental research designs can and should be established to test the effectiveness of marine reserves simultaneously with other measures.

Institutional structures can result in resistance to using marine reserves. Agencies that focus almost exclusively on single species or fisheries, for example, are often discouraged from using marine reserves because of complications involving different species, bycatch from other fisheries and interactions with other agencies. By narrowly focusing on specific fishery problems, some agencies neglect other conservation, aesthetic, ecological and recreational issues. Establishment of marine reserves in the Florida Keys National Marine Sanctuary, for example, became complicated by issues involving state and federal authority, and conflicts between different fishery and sanctuary conservation goals (Bohnsack 1997).

DISCUSSION AND CONCLUSIONS

There is growing interest in establishing marine reserves to protect representative parts of marine ecosystems as a hedge against our ignorance based on the precautionary principle (Ballantine 1994, 1995; Dayton *et al.* 1995). Recommendations include establishing networks of 'no-take' reserves with all representative habitats. Ballantine (1994, 1995) emphasized the critical need to allow non-consumptive use in these areas in order to foster continued public support, encourage compliance and advance our scientific understanding of marine ecosystems. He further suggested that primary goals should be to leave some areas undisturbed for their intrinsic worth to present and future generations, to provide critical reference points for evaluating the effects of human activities on ecosystems, and to provide increased understanding of ecosystems; and not just to increase some net yield for human consumption. These arguments may be convincing in developed countries that are not totally dependent on their coastal fisheries, where fisheries are not fully exploited and where the population is highly educated. However, goals of having a 'better understanding of marine ecosystems' or 'protecting areas for their intrinsic worth' are not likely to be convincing to the hungry and unemployed. For these reasons, practical benefits of marine reserves will need to be 'proven' before they can be widely used. Fishery science has an important role to play in this effort but it will require the leadership and support of the more developed countries.

In conclusion, no-take marine reserves are a promising management tool that can be used in conjunction with traditional fishery management methods to holistically manage marine resources. Progress in establishing and evaluating marine reserves will be difficult because of the complex biological, physical, social and economic factors that must be considered. The research questions posed in this paper should have a high

level of scientific and management interest. However, uncertainty should not be used as a reason against establishing marine reserves, especially in developed countries. In most regions, sufficient knowledge currently exists to develop and use reserves effectively, particularly in an adaptive management approach of learning from mistakes (Roberts *et al.* 1995).

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REFERENCES

- Alder J. (1996) Have tropical marine protected areas worked? An initial analysis of their success. *Coastal Manag.* **24**, 97–114.
- Alder J., Sloan N. A. & Uktolseya H. (1994) A comparison of management planning and implementation in three Indonesian marine protected areas. *Ocean Coast. Manag.* **24**, 179–98.
- Angermeier P. L. & Schlosser I. J. (1995) Conserving aquatic biodiversity: Beyond species and populations. *Am. Fish. Soc. Symp.* **17**, 402–14.
- Apollonio S. (1994) The use of ecosystem characteristics in fisheries management. *Rev. Fish. Sci.* **2**, 157–80.
- Appeldoorn R. (1996) Model and method in reef fishery assessment. In: *Reef Fisheries*, Fish and Fisheries Series 20 (eds N. V. C. Polunin & C. M. Roberts) pp. 219–48. Chapman and Hall, London.
- Attwood C. G. & Bennet B. A. (1994) Variation in dispersal of Galjoen (*Coracinus capensis*) (Teleostei: Coracinae) from a marine reserve. *Can. J. Fish. Aquat. Sci.* **51**, 1247–57.
- Ballantine B. (1991) Marine reserves for New Zealand. University of Auckland, *Leigh Lab. Bull.* **25**, 1–196.
- Ballantine W. J. (1994) Networks of 'no-take' marine reserves are practical and necessary. In: *Marine Protected Areas and Sustainable Fisheries*, (eds N. L. Shackell & J. H. M. Willison) pp. 13–20. Science and Management of Protected Areas Association, Wolfville, Nova Scotia.
- Ballantine W. J. (1995) The New Zealand experience with 'no-take' marine reserves. In: *Review of The Use of Marine Fishery Reserves in The US Southeastern Atlantic* (eds C. M. Roberts, W. J. Ballantine, C. D. Buxton *et al.*) pp. 15–31. NOAA Tech. Memo. NMFS-SEFSC-376.
- Bergh M. O. & Getz W. M. (1989) Stability and harvesting of competing populations with genetic variation in life history strategy. *Theor. Popul. Biol.* **36**, 77–124.
- Bohnsack J. A. (1993) Marine reserves: They enhance fisheries, reduce conflicts, and protect resources. *Oceanus* **36**, 63–71.
- Bohnsack J. A. (1994) How marine fishery reserves can improve reef fisheries. *Proc. Gulf Caribb. Fish. Inst.* **43**, 217–41.
- Bohnsack J. A. (1996) Maintenance and recovery of fishery productivity. In: *Tropical Reef Fisheries*, Fish and Fisheries Series 20 (eds N. V. C. Polunin & C. M. Roberts) pp. 283–313. Chapman and Hall, London.
- Bohnsack J. A. (1997) Consensus development and the use of marine reserves in the Florida Keys, USA. *Proc. 8th Int. Coral Reef Symp.* **2**, 1927–30.
- Bohnsack J. A. & Ault J. S. (1996) Management strategies to conserve marine biodiversity. *Oceanography* **9**, 72–82.
- Buxton C. D. (1993) Life-history changes in exploited reef fishes on the east coast of South Africa. *Env. Biol. Fish.* **36**, 47–63.
- Carr M. H. & Reed D. C. (1993) Conceptual issues relevant to marine harvest refuges: Examples from temperate reef fishes. *Can. J. Fish. Aquat. Sci.* **50**, 2019–28.
- Christensen N. L., Bartuska A. M., Carpenter S. *et al.* (1996) The report of the Ecological Society of America Committee on the scientific basis for ecosystem management. *Ecol. Appl.* **6**, 665–91.
- Cole R. G., Ayling T. M. & Creese R. G. (1990) Effects of marine reserve protection at Goat Island, northern New Zealand. *NZ J. Mar. Freshwat. Res.* **24**, 197–210.
- Cole-King A. (1995) Marine protected areas in Britain: a conceptual problem? *Ocean Coast. Manag.* **27**, 109–127.
- Davis G. E. (1989) Designated harvest refugia: the next stage of marine fishery management in California. *Calif. Coop. Oceanic Fish. Invest. Rep.* **30**, 53–8.
- Davis G. E. & Dodrill J. W. (1980) Marine parks and sanctuaries for spiny lobster fisheries management. *Proc. Gulf Caribb. Fish. Inst.* **32**, 194–207.
- Dayton P. K., Thrush S. F., Agardy M. T. & Hofman R. J. (1995) Environmental effects of marine fishing. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* **5**, 1–28.
- Dugan J. E. & Davis G. E. (1993) Applications of marine refugia to coastal fisheries management. *Can. J. Fish. Aquat. Sci.* **50**, 2029–42.
- Duran L. R. & Castilla J. C. (1989) Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. *Mar. Biol.* **103**, 555–62.
- FAO (1994) Review of the state of world marine fishery resources. *FAO Fish. Tech. Pap.* **335**, 1–136.
- Gubbay S. (1995) *Marine Protected Areas: Principles and Techniques for Management*. Chapman and Hall, London.
- Halas L. S. Jr & Reitz E. J. (1992) Historical changes in age and growth of Atlantic Croaker, *Micropogonias undulatus* (Perciformes: Sciaenidae). *J. Arch. Sci.* **19**, 73–99.
- Holland D. S. & Brazee R. J. (1996) Marine reserves for fisheries management. *Mar. Res. Econ.* **11**, 157–71.
- Holling C. S. & Meffe G. K. (1996) Command and control and the pathology of natural resource management. *Conserv. Biol.* **10**, 328–37.
- Jennings S., Marshall S. S. & Polunin N. V. C. (1996) Seychelles' marine protected areas: Comparative structure and status of reef fish communities. *Biol. Conserv.* **75**, 201–9.
- Kunzig R. (1995) Twilight of the Cod. *Discover* **95**(4), 44–58.
- Lozano-Alvarez E., Briones-Fourzan P. & Negrete-Soto F. (1993) Occurrence and seasonal variations of spiny lobsters, *Panulirus argus* (Latreille), on the shelf outside Bahia de la Ascension, Mexico. *Fish. Bull. US* **91**, 808–15.
- Ludwig D., Hilborn R. & Walters C. (1993) Uncertainty, resource exploitation, and conservation: Lessons from history. *Science* **260**, 17–18.
- McAllister M. K. & Peterman R. M. (1992) Decision analysis of a large-scale fishing experiment designed to test for a genetic effect of size-selective fishing on British Columbia pink salmon (*Oncorhynchus gorbuscha*). *Can. J. Fish. Aquat. Sci.* **49**, 1305–14.
- McClanahan T. R. (1994) Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins. *Coral Reefs* **13**, 231–41.
- McClanahan T. R. (1995) A coral reef ecosystem-fisheries model: impacts of fishing intensity and catch selection on reef structure and processes. *Ecol. Model.* **80**, 1–19.
- McClanahan T. R. & Mutiga N. A. (1988) Changes in Kenyan

- coral reef community structure and function due to exploitation. *Hydrobiologia* **166**, 269–76.
- MacDiarmid A. B. & Breen P. A. (1992) Spiny lobster population changes in a marine reserve. In: *Proc. 2nd Int. Temp. Reef Symp.* (eds C. N. Battershill *et al.*) pp. 47–56. NIWA Marine, Wellington, New Zealand.
- Miller L. M. & Kapuscinski A. R. (1994) Estimation of selection differentials from fish scales: A step towards evaluating genetic alteration of fish size in exploited populations. *Can. J. Fish. Aquat. Sci.* **51**, 774–83.
- Montgomery W. L. (1983) Parr excellence. *Nat. Hist.* **6/83**, 58–67.
- Munro J. L. & Williams D. M. (1985) Assessment and management of coral reef fisheries: Biological, environmental, and socio-economic aspects. *Proc. 5th Int. Coral Reef Congr.* **4**, 544–78.
- Murawski S. A. (1991) Can we manage our multispecies fisheries? *Fisheries* **16**, 5–13.
- National Research Council (1994) *Improving The Management of US Marine Fisheries*. National Academy Press, Washington DC.
- Nelson K. & Soulé M. (1987) Genetical conservation of exploited fishes. In: *Population Genetics and Fishery Management* (eds N. Ryman & F. Utter) pp. 345–68. University of Washington Press, Seattle.
- Nowlis J. S. (1995) Quantitative and qualitative predictions of optimal fishery reserve design (abstract). In: *Proceedings of the American Fisheries Society 125th Annual Meeting*, Tampa, FL, August 27–31, p. 28.
- Parma A. M. & Deriso R. B. (1990) Dynamics of age and size composition in a population subject to size-selective mortality: Effects of phenotypic variability in growth. *Can. J. Fish. Aquat. Sci.* **47**, 274–89.
- Plan Development Team (1990) *The Potential of Marine Fisheries Reserves for Reef Management in the US Southern Atlantic*. (ed. J. A. Bohnsack). NOAA Tech. Mem. NMFS-SEFSC-261.
- Pulliam H. R. (1988) Sources, sinks, and population regulation. *Am. Nat.* **132**, 652–61.
- Ramos-Espla A. A. & McNeill S. E. (1994) The status of marine conservation in Spain. *Ocean Coast. Manag.* **24**, 125–38.
- Ricker W. E. (1981) Changes in the average size and average age of Pacific salmon. *Can. J. Fish. Aquat. Sci.* **38**, 1636–56.
- Roberts C. M. (1997) Ecological advice for the global fisheries crisis. *Trends Evol. Ecol.* **12**, 35–8.
- Roberts C., Ballantine W. J., Buxton C. D. *et al.* (1995) Review of the use of marine fishery reserves in the US Southeastern Atlantic. NOAA Tech. Mem. NMFS-SEFSC-376.
- Roberts C. M. & Polunin N. V. C. (1991) Are marine reserves effective in management of reef fisheries? *Rev. Fish. Biol. Fish.* **1**, 65–91.
- Roberts C. M. & Polunin N. V. C. (1993) Marine reserves: Simple solutions to managing complex fisheries? *Ambio* **22**, 363–8.
- Rowley R. J. (1994) Case studies and reviews: Marine reserves in fisheries management. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* **5**, 233–54.
- Russ G. R. & Alcala A. C. (1994) Sumilon Island Reserve: 20 years of hopes and frustration. *NAGA, ICLARM Quart.* **17**, 8–12.
- Russ G. R. & Alcala A. C. (1996a) Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Mar. Ecol. Prog. Ser.* **132**, 1–9.
- Russ G. R. & Alcala A. C. (1996b) Marine reserves: Rates and patterns of recovery and decline of large predatory fish. *Ecol. Appl.* **6**, 947–61.
- Savina C. (1995) The world's imperiled fish. *Sci. Am.* **273**, 46–53.
- Shackell N. L. & Willison J. H. M. (eds) (1995) *Marine Protected Areas and Sustainable Fisheries*. Science and Management of Protected Areas Association, Wolfville, Nova Scotia.
- Shafer C. L. (1990) *Nature Reserves: Island Theory and Conservation Practice*. Smithsonian Institution Press, Washington DC.
- Sheridan A. K. (1995) The genetic impacts of human activities on wild fish populations. *Rev. Fish. Sci.* **3**, 91–108.
- Shulman M. J. & Bermingham E. (1995) Early life histories, ocean currents, and the population genetics of Caribbean reef fishes. *Evolution* **49**, 897–10.
- Simberloff D. S. & Abele L. G. (1976) Island biogeography theory and conservation practice. *Science* **191**, 285–6.
- Smith P. J., Francis R. I. C. C. & McVeagh M. (1991) Loss of genetic diversity due to fishing pressure. *Fish. Res.* **10**, 309–16.
- Stoner A. W. & Ray M. (1996) Queen conch, *Strombus gigas*, in fished and unfished locations of the Bahamas: effects of a marine fishery reserve on adults, juveniles, and larval production. *Fish. Bull. US* **94**, 551–65.
- Thorpe J. E., Koonce J. F. *et al.* (1981) Assessing and managing man's impact on fish genetic resources. *Can. J. Fish. Aquat. Sci.* **38**, 1899–1907.
- Tisdell C. & Broadus J. M. (1989) Policy issues related to the establishment and management of marine reserves. *Coast Manag.* **17**, 37–53.
- Towns D. R. & Ballantine W. J. (1993) Conservation and restoration of New Zealand island ecosystems. *Trends Evol. Ecol.* **8**, 452–7.
- Travis J. (1989) The role of optimizing selection in natural populations. *Ann. Rev. Ecol. Syst.* **20**, 279–96.
- Waters J. R. (1991) Restricted access *vs* open access methods of management: Toward more effective regulation of fishing effort. *Mar. Fish. Rev.* **53**, 1–10.
- Wilson D. S. & Clarke A. B. (1996) The shy and the bold. *Nat. Hist.* **9/96**, 26–8.
- Wolfenden J., Cram F. & Kirkwood B. (1994) Marine reserves in New Zealand: A survey of community reactions. *Ocean Coast. Manag.* **25**, 31–51.